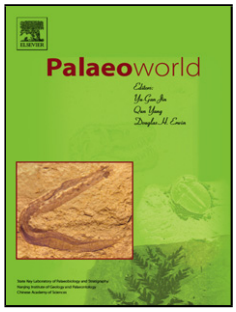

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PII: S1871-174X(18)30164-1
DOI: https://doi.org/10.1016/j.palwor.2019.03.002
Reference: PALWOR 496

To appear in: *Palaeoworld*

Received date: 20 November 2018
Revised date: 11 January 2019
Accepted date: 22 March 2019

Please cite this article as: Huang, Bing, Zhou, Hang-Hang, Harper, David A.T., Zhan, Ren-Bin, Zhang, Xiao-Le, Chen, Di, Rong, Jia-Yu, A latest Ordovician Hirnantia brachiopod fauna from western Yunnan, Southwest China and its paleobiogeographic significance.Palaeoworld https://doi.org/10.1016/j.palwor.2019.03.002

A latest Ordovician *Hirnantia* brachiopod fauna from western Yunnan, Southwest China and its paleobiogeographic significance

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Abstract

A new, high-diversity, latest Ordovician brachiopod fauna of nearly 800 brachiopod specimens was collected from the Wanyaoshu Formation (Hirnantian) in the Shaodihe section, Mangshi City, western Yunnan, Southwest China. Altogether 22 genera and two undetermined taxa were identified; dominant are *Aegiromena*, *Anisopleurella*, *Fardenia*, *Dalmanella*, *Hirnantia* and *Hindella*, less common, *Paromalomena*, *Leptaena*, *Eostropheodonta*, *Cliftonia*, *Kinnella*, *Templeella* and *Plectothyrella*, together with some rare *Petrocrania*, *Xenocrania*, *Pseudopholidops*, *Palaeoleptostrophia*, *Skenidioides*, *Giraldibella*, *Draborthis*, *Dolerorthis* and *Toxorthis*. This is one of the most diverse typical *Hirnantia* faunas, associated with the Kosov Province. The paleobiogeographic relationships between western Yunnan (Southwest China), Myanmar, Yichang (Central China), Tibet (Southwest China) and Kazakhstan are clarified using Network Analysis and NMDS. The fauna studied is most similar to

that of Myanmar; both resided on the Sibumasu terrane. However, the recalculated network diagram, when including the data of *Hirnantia* fauna from the Prague Basin, indicates that the latter is more closely linked to that of western Yunnan, a testament to the very weak brachiopod provincialism during the Hirnantian, mainly due to the influence of dominant cosmopolitan taxa. Some species of the fauna display significant population variation. Two of the dominant taxa, *Aegiromena* and *Anisopleurella* are systematically described, whereas the other two common taxa, *Fardenia* and *Hirnantia* are measured and their outlines and internal structures analyzed.

Keywords: *Hirnantia* brachiopod fauna; latest Ordovician; western Yunnan; China; Sibumasu

1. Introduction

The latest Ordovician *Hirnantia* fauna is, geographically, the widest-distributed brachiopod fauna in the entire Phanerozoic (Rong et al., 2017). It has been documented from many places throughout the world, including most plates and terranes. Among them, the fauna from the Sibumasu terrane was first described more than 100 years ago (Reed, 1915) and was first recognized as a member of the *Hirnantia* fauna half a century later (Temple, 1965). The Sibumasu terrane extends from Malaysia, through peninsular Thailand, Myanmar to western Yunnan. To date, the *Hirnantia* fauna of this terrane has been described in detail only from Thailand (Cocks and Fortey, 1997) and Myanmar (Reed, 1915; Cocks and Fortey, 2002; Rong et al., in press).

Rong and Sun (1983) reported a diverse *Hirnantia* fauna near the Mangjiu Reservoir (locality number ACJ-906) in Luxi City (now Mangshi City), western Yunnan, Southwest China in a conference abstract listing 15 brachiopod species without illustrations. Recently, Fang et al. (2018) discussed in detail the biostratigraphy of the succession within the Upper Ordovician in the Baoshan and Mangshi regions, both from western Yunnan. They reported a *Hirnantia* fauna in the Shaodihe section containing seven species identified by one of the authors (Rong, J.Y.). At the same locality, the first two authors of the paper together with their colleagues collected a

large number of shelly fossils from the upper Wanyaoshu Formation at the end of 2017. The brachiopods are the most abundant, comprising almost the whole fauna and containing 22 named taxa along with two undetermined species. In addition to the genera recorded by Rong and Sun (1983) and Fang et al. (2018), there occur nine more genera: *Pseudopholidops*, *Petrocrania*, *Xenocrania*, *Eostropheodonta*, *Palaeoleptostrophia*, *Skenidioides*, *Giraldibella*, *Dolerorthis*, *Templeella* and some others, which are reported from western Yunnan for the first time. This is one of the most diverse, typical *Hirnantia* faunas. In addition to brachiopods, the fauna includes many major animal groups, e.g., trilobites, bryozoans, crinoid debris, gastropods, corals, bivalves, machaeridians and a few others.

The Mangshi Region of western Yunnan was part of the Sibumasu terrane during the Ordovician and Silurian (Metcalfe, 2011). Geologically, the Ordovician and Silurian rocks of the Mangshi Region are similar to those in the Shan State of Myanmar (Cocks and Fortey, 2002). Coincidently, a recently discovered *Hirnantia* fauna from the Mandalay Division, Myanmar (Rong et al., in press) with a high diversity (23 species) is closely comparable to this fauna. In this study, the brachiopod species recovered are illustrated, two typical species *Aegiromena* (*Aegiromenella*) cf. *planissima* and *Anisopleurella asiatica* are described systematically, and two common species *Hirnantia sagittifera* (M'Coy, 1851) and *Fardenia* (*Coolinia*) cf. *dalmani* Bergström, 1968 are measured and regression analyses presented. The paleogeographic significance of the fauna is discussed by comparing the data from Myanmar (Sibumasu terrane), South China, Xainza (Lhasa paleoplate), Kazakhstania and Prague, using Network Analysis.

2. Locality, material and geological setting

Most of the specimens were collected recently from the Shaodihe section together with a few specimens from the Mangjiu Reservoir obtained by Rong and Sun (1983). The section in the Mangjiu Reservoir (ACJ-906) can no longer be located based on available information and is now probably partly below water due to flooding of the reservoir. The Shaodihe section, however, is located near Dakuangshan quarry, about 7

km northeast of Mangshi City, western Yunnan, Southwest China (GPS: 24°28'07.2"N, 98°38'46.2"E) (Fig. 1). The fossils are mainly concentrated in two layers (lower YMS-01 and upper YMS-02) in the upper Wanyaoshu Formation. Collections from between the two beds (YMS-02a and YMS-02b) and below YMS-01 (YMS-01a, YMS-01b and YMS-01c) were also made (Fig. 2). We collected 793 brachiopod specimens, which are preserved as external and internal moulds.

Identifications of the brachiopods from seven beds indicate the presence of eight orders, including the Craniopsida, Craniida, Strophomenida, Orthotetida, Protorthida, Orthida, Rhynchonellida and Athyridida, represented by 22 genera. The associations are grouped into lower and upper assemblages. Both assemblages contain *Hirnantia*, *Kinnella*, *Dalmanella* and some other typical components of the *Hirnantia* fauna. The lower assemblage is dominated by *Fardenia*, *Hirnantia* and *Hindella*, while the upper one by *Aegiromena*, *Anisopleurella* and *Dalmanella*. Significantly, orthides dominate in both abundance and generic diversity. Ecological analysis of the two assemblages will be fully discussed in another paper, which focuses on the environmental transition from shallow to deeper water in the *Hirnantia* fauna. This study will mainly report and illustrate the fauna and discuss its paleobiogeographic significance.

The Wanyaoshu Formation, at the Shaodihe section, containing the *Hirnantia* fauna, is composed of yellowish-green medium to thickly-bedded silty mudstone intercalated with a few siltstones, and with pale mudstone near the top. The formation is overlain by the Jenhochiao Formation (uppermost Ordovician to lower Silurian) and underlain by the Luxi Formation. The published geological information available for the section indicates that the Wanyaoshu Formation is about 12 m thick (Fang et al., 2018, fig. 2). However, we collected and measured only 5.85 m of the upper part of the formation. The lower part and the underlying Luxi Formation are no longer accessible due to massive excavations at the locality. Graptolites collected from the base of the Jenhochiao Formation were assigned to the upper Hirnantian *M. extraodinarius* and *M. persculptus* biozones. However, the first occurrence of *M. extraordinarius* in this section does not necessarily indicate the true FAD of the species; the base of the Jenhochiao Formation may be higher than the *M. extraordinarius* Biozone (Fang et al.,

2018). The brachiopod assemblage collected from the upper Wanyaoshu Formation is dominated by *Anisopleurella* and *Aegiromena*, which are usually considered deep-water taxa. Compared to the lower assemblage containing shallow-water indicators, such as very large shell size (more than 40 mm), high abundance and lower diversity, the upper assemblage suggests an increased water depth corresponding to the global warming and associated sea level rise, during the late Hirnantian. Here we assign the top of the Wanyaoshu Formation to the lower *M. persculptus* biozone.

3. Paleobiogeographical significance

Brachiopods can be assigned to four provinces (tropical East Gondwana, Baltica, Laurentia–Siberia and Mediterranean) during most of the Ordovician (Harper and Servais, 2013; Torsvik and Cocks, 2017). However, the provincialism in the benthic faunas declined as the Ordovician progressed, especially after the first phase of the end Ordovician mass extinction (Harper et al., 2013). The western Yunnan and the Myanmar together form the northern part (current orientation) of the Sibumasu terrane (Metcalfe, 2011). Not surprisingly, the *Hirnantia* fauna from the two regions are very similar. Besides the close paleobiogeographic relationships between the two regions of the Sibumasu terrane, there are also links with other areas indicated by a number of more exotic taxa (see Rong et al., in press). Here, we use a Network diagram to illustrate the paleobiogeographic net connecting Mangshi in western Yunnan, and Mandalay in Myanmar, Yichang in South China paleoplate (Rong, 1984), Xainza in Lhasa paleoplate (Rong and Xu, 1987) and Chu-Ili in Kazakhstan (Nikitin et al., 1980), all of which were once part of the tropical east Gondwana province (Fig. 3A). The paleomap shows the geographic relationship between those localities.

The Network diagram (Fig. 3B) clearly indicates the mutual geographic relationships between the five plates or terranes. Both Yichang and Kazakhstan have more endemic taxa than other regions, and display a relative independence, whereas western Yunnan and Mandalay share the most genera and show the closest relationships due to their close geographic proximity. Although the diversity of the *Hirnantia* fauna from Xainza is limited, which may be due to insufficient sampling; a closer relationship

with South China and Sibumasu than with Kazakhstan is indicated. However, relatively large numbers of *Anisopleurella* in the fauna from Chu-Ili (Nikitin et al., 1980) render its comparability with the upper assemblage in the Shaodihe section, western Yunnan; but it cannot be detected by the Network analysis.

The *Hirnantia* fauna reported here and that of Myanmar are very similar to that of the Yichang area, western Hubei, Central China (Rong, 1984; Zeng et al., 2016) since they share many common genera and/or species. However, the *Hirnantia* fauna from the Prague Basin, Bohemia (Marek and Havlíček, 1967) shows even higher similarity to that from Yichang area as they have more genera in common (Rong et al., in press). We added the Bohemia data into the network, and used NMDS to confirm this relationship (Fig. 4). The topology of the net diagram for the five plates or terranes is unchanged, and the node for Bohemia indicates a close relationship with the data from this study. There are five cosmopolitan genera *Eostropheodonta*, *Cliftonia*, *Dalmanella*, *Hirnantia* together with *Aegiriomena* distributed in all regions, forming a pentagon in the diagram for the five plates or terranes; the pattern of the diagram did not change with the addition of data from Bohemia (Fig. 4).

In fact, among the key or common taxa of the *Hirnantia* fauna, whether in western Yunnan, Myanmar or in Yichang area, there is a suite of cosmopolitan genera recorded from many parts of the world, for example, *Leptaena*, *Paromalomena*, *Eostropheodonta*, *Fardenia*, *Cliftonia*, *Dalmanella*, *Hirnantia*, *Kinnella*, *Plectothyrella*, and *Hindella*. Provincial signals within the *Hirnantia* fauna are generally weak. Most of the typical components of the *Hirnantia* fauna are cosmopolitan. The provincialism detected, however, may be due to poor correlation (e.g., with Edgewood fauna, see Wang et al., 2018), or different facies, rather than due to its paleogeographical distribution. This will be discussed in more detail by Rong et al. in a forthcoming review paper.

4. Systematic paleontology

All the specimens illustrated are registered in the collections of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (the numbers

prefixed by NIGP). The fauna is most similar to that of Myanmar, whose components are described systematically by Rong et al. (in press). We will not describe those taxa here. The list of species reported in this study is as follows, with some representative specimens being illustrated: *Pseudopholidops partibilis* (Rong, 1979) (Fig. 5A), *Xenocrania haimei* (Reed, 1915) (Fig. 5B–D, G), *Petrocrania* sp. (Fig. 5E, F), *Leptaena rugosa* (Dalman, 1828) (Fig. 6A–F), *Paromalomena mcmahoni* (Reed, 1915) (Fig. 6G–O), *Eostropheodonta hirnantensis* (M'Coy, 1851) (Fig. 7A–C), *Palaeoleptostrophia* sp. (Fig. 7D–F), *Aegiromena* (*Aegiromenella*) cf. *planissima* (Reed, 1915) (Fig. 8I–O), *Anisopleurella asiatica* Rong et al., 2013 (Fig. 8A–H), *Fardenia* (*Coolinia*) cf. *dalmani* Bergström, 1968 (Fig. 11A–K), *Cliftonia* cf. *psittacina* (Wahlenberg, 1821) (Fig. 11L–O), *Skenidioides* cf. *scoliodus* Temple, 1968 (Fig. 13A), *Dolerorthis*? sp. (Fig. 13D, E), *Giraldibella* sp. (Fig. 13C, F), *Toxorthis*? sp. (Fig. 13B), *Dalmanella testudinaria* (Dalman, 1828) (Fig. 13K–R), *Templeella* cf. *gobiensis* Rozman and Rong, 1993 (Fig. 13G–J), *Draborthis caelebs* Marek and Havlíček, 1967 (Fig. 15E, F), *Kinnella medlicotti* (Reed, 1915) (Fig. 15A–D), *Hirnantia sagittifera* (M'Coy, 1851) (Fig. 15G–R), *Plectothyrella crassicostis* (Dalman, 1828) (Fig. 16A–H), *Hindella crassa* (Sowerby, 1839) (Fig. 16I–M).

Among the species listed above, *Aegiromena* (*Aegiromenella*) cf. *planissima* (Reed, 1915) and *Anisopleurella asiatica* Rong et al., 2013, dominating the upper assemblage of the *Hirnantia* fauna in the Shaodihe section, are described here in detail. Since *Hirnantia sagittifera* (M'Coy, 1851) and *Fardenia* (*Coolinia*) cf. *dalmani* Bergström, 1968 from Myanmar are described by Rong et al., (in press); only measurements, bivariate graphs and regression analyses derived from present collection are provided here for comparison. For *Dolerorthis*? sp. and *Giraldibella* sp., only two specimens of each species are available which do not warrant description. *Templeella* cf. *gobiensis* Rozman and Rong, 1993 is absent in Myanmar. There are only four records globally of this specialized dalmanelloid, which is the only representative of its subfamily. The specimens of *Templeella* cf. *gobiensis* in this study will be described and discussed elsewhere.

Order Strophomenida Öpik, 1934

Superfamily Plectambonitoidea Jones, 1928

Family Xenambonitidae Cooper, 1956

Subfamily Aegiromeninae Havlíček, 1961

Genus *Aegiromena* Havlíček, 1961

Subgenus *Aegiromena* (*Aegiromenella*) Rong et al., 2013

Aegiromena (*Aegiromenella*) cf. *planissima* (Reed, 1915)

(Fig. 8I–O)

pars 1915 *Schuchertella planissima* – Reed, p. 78, pl. 11, figs. 13–16, 18, 19, non fig. 17.

1984 *Aegiromena ultima* Marek and Havlíčk – Rong, p. 150, pl. 11, figs. 10, 13.

non 1997 *Aegiromena planissima* (Reed) – Cocks and Fortey, p. 124, pl. 2, figs. 9–18.

2002 *Aegiromena*? *planissima* (Reed) – Cocks and Fortey, p. 71, pl. 4, figs. 4–11.

2013 *Aegiromena* (*Aegiromenella*) *planissima* – Rong et al., p. 48, figs. 33–45.

Material: Sixty-five specimens; internal and external moulds of both valves.

Description:

Exterior. Shell minute (1.4–3.6 mm long, 2.6–6.6 mm wide), semicircular in outline, 50%–70% of shell length as width; cardinal extremities generally rectangular, weakly concavo-convex; hinge line straight. Ventral valve slightly convex at umbo; dorsal valve weakly concave, beak inconspicuous. Ornament parvicostellate, variable (Fig. 8O), of 5–7 strong primary ribs arising at umbo, occasionally one secondary rib intercalated, and 2–3 finer radial lines between primary (or secondary) ribs; on average 6–8 ribs per mm at anterior margin (shells ca. 5 mm wide), with up to 10 per mm finer ribs, arising mainly by intercalation.

Ventral interior. Dental plates thin, very short or vestigial, widely divergent; muscle scars commonly 20%–25% shell width, defined postero-laterally by fine and low

bounding ridges, but poorly-defined anteriorly, apparently bilobed (Fig. 8J), bisected by weak short myophragm.

Dorsal interior. Socket plates short, divergent mostly at 130°–150° or rarely almost parallel to hingeline; bema almost lacking or very weak; a long, narrow median septum extending to approximately 60%–70% of valve length (Fig. 8M, N).

Remarks: The subgenus *Aegiromena* (*Aegiromenella*) was established with special reference to its typical, indistinct or poorly-defined bema (Rong et al., 2013). The specimens in this study have not retained a bema, or more rarely the bema is weakly impressed (Fig. 8L), and thus can be assigned to the nominate subgenus. The species of *A.* (*Aegiromenella*), common in the Katian and the Hirnantian stages, are mainly in BA4–5, deeper-water environments. Besides the type species *A. planissima* Reed, 1915, there are two more Hirnantian species, *A. durbenensis* Nikitin et al. (1980) from the Durben Horizon (Hirnantian), Durben, Chu-Ili Mountains, Kazakhstan, and *A. ultima* Havlíček (1967) from the Kosov Formation (Hirnantian), Bechovice, Czech Republic. *A. ultima* commonly bears a very weak bema, and the dental plates of *A. durbenensis* are less divergent and well developed, which differ from our specimens; consequently, we assign our specimens to *A. planissima*. However, the ornamentation of the specimens in this study is more variable than that of the type species, and we identify them as *A.* (*A.*) cf. *planissima*.

Measurements and statistics: Complete specimens have been measured and analyzed by bivariate regression, see Table 1 and Fig. 9.

Family Sowerbyellidae Öpik, 1930

Subfamily Sowerbyellinae Öpik, 1930

Genus *Anisopleurella* Cooper, 1956

Anisopleurella asiatica Rong et al., 2013

(Fig. 8A–H)

2008 *Anisopleurella* sp. Rong et al., fig. 4d, e.

2013 *Anisopleurella asiatica* – Rong et al., fig. 35.

Material: Ninety-six specimens, external and internal moulds of ventral and dorsal valves.

Description:

Exterior. Small shells, outline variable, transversely semioval to semicircular, 45%–88% as long as wide, ventral valve strongly convex and evenly rounded, most convex just in front of mid-valve; dorsal valve deeply concave. Ornament of very fine parvicostellae on ventral valve, commonly three to rarely five thicker primary costae; many fine capillae in between, about 10 per mm.

Ventral interior. Teeth minute, dental plates absent; muscle field short, poorly-defined anterolaterally; median myophragm not seen; pair of vascula media narrow and short, slightly impressed, diverging forwards at about 60°–85°.

Dorsal interior. Cardinal process undercut, minute and linear, located transversely (Fig. 8D, E), ankylosed laterally with elongate socket ridges lying nearly parallel to hingeline and defining very narrow, small transverse sockets; median septum slender, extending anteriorly for 50%–75% of valve length; bema usually lacking a clear margin (Fig. 8E), adductor scars somewhat suboval, faint; side septa prominent and high, diverging anteriorly at angle of 65°–70°, central side septa shorter and finer than side septa, subtending angle of 15°–20° as lateral bounding ridges of muscle scars.

Remarks: Rong et al. (2013) erected the species *Anisopleurella asiatica* based on the specimens collected from the top of the Yankou Formation (uppermost Hirnantian) of south-east China (AGI 296–303). Both the internal and external architecture of the holotype and paratypes are similar to our specimens especially the dorsal internal moulds, although the range of variation is slightly larger than that of type specimens in outline, length of median septum and angle between the side septa. This variation is partly a consequence of the large sample size available for this study compared to that from south-east China (96 versus 46). Nevertheless, the specimens in this study were collected from the uppermost Wanyaoshu Formation, a close correlative of the top of the Yankou Formation in south-east China.

Measurements and statistics: Complete specimens have been measured and a regression analysis of these data is presented, see Table 2 and Fig. 10.

Order Orthotetida Waagen, 1884

Suborder Orthotetidina Waagen, 1884

Superfamily Chilidiopsoidea Boucot, 1959

Family Chilidiopsidae Boucot, 1959

Genus *Fardenia* Lamont, 1935

Subgenus *Fardenia* (*Coolinia*) Bancroft, 1949

Fardenia (*Coolinia*) cf. *dalmani* Bergström, 1968

(Fig. 11A–K)

Remarks: For synonymy lists and description, see Rong et al. (in press). The specimens in this study are commonly larger than those of Myanmar, particularly the largest specimens (45.7 mm width versus 30 mm width for the Myanmar specimens).

Measurements and statistics: Complete specimens have been measured and a regression analysis of these data is presented, see Table 3 and Fig. 12.

Order Orthida Schuchert and Cooper, 1932

Superfamily Enteletoidea Waagen, 1884

Family Draboviidae Havlíček, 1950

Subfamily Draboviinae Havlíček, 1950

Genus *Hirnantia* Lamont, 1935

Hirnantia sagittifera (M'Coy, 1851)

(Fig. 15G–R)

Remarks: For a comprehensive synonym list and discussion see Rong et al. (in press). Remarkably, the largest brachiopod shell is a dorsal internal mould of *Hirnantia*

sagittifera reaching almost 48 mm in width.

Measurements and statistics: Complete specimens are measured and a regression analysis of these data is presented, see Table 4 and Fig. 14.

Acknowledgments

The authors would like to thank Drs. Fang Xiang and Mu Lin (NIGP, Chinese Academy of Sciences) for providing information about the section and help during fieldwork, respectively. The comments of Robin Cocks and an anonymous referee together with those of the editor greatly improved the clarity of the manuscript. Financial support for this study was provided by the National Natural Science Foundation of China (NSFC) Nos. 41472006 and 41530103; the Strategic Priority Research Program of Chinese Academy of Sciences, Grant No. XDB 26000000; Harper acknowledges support from the Leverhulme Trust (UK). This is a contribution to IGCP Project 653 'The Onset of the Great Ordovician Biodiversification Event'.

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Figure and table captions

Fig. 1. Location map showing the Shaodihe section and Mangjiu Reservoir section in Mangshi City, western Yunnan, Southwest China, where the *Hirnantia* fauna documented in this paper occurs.

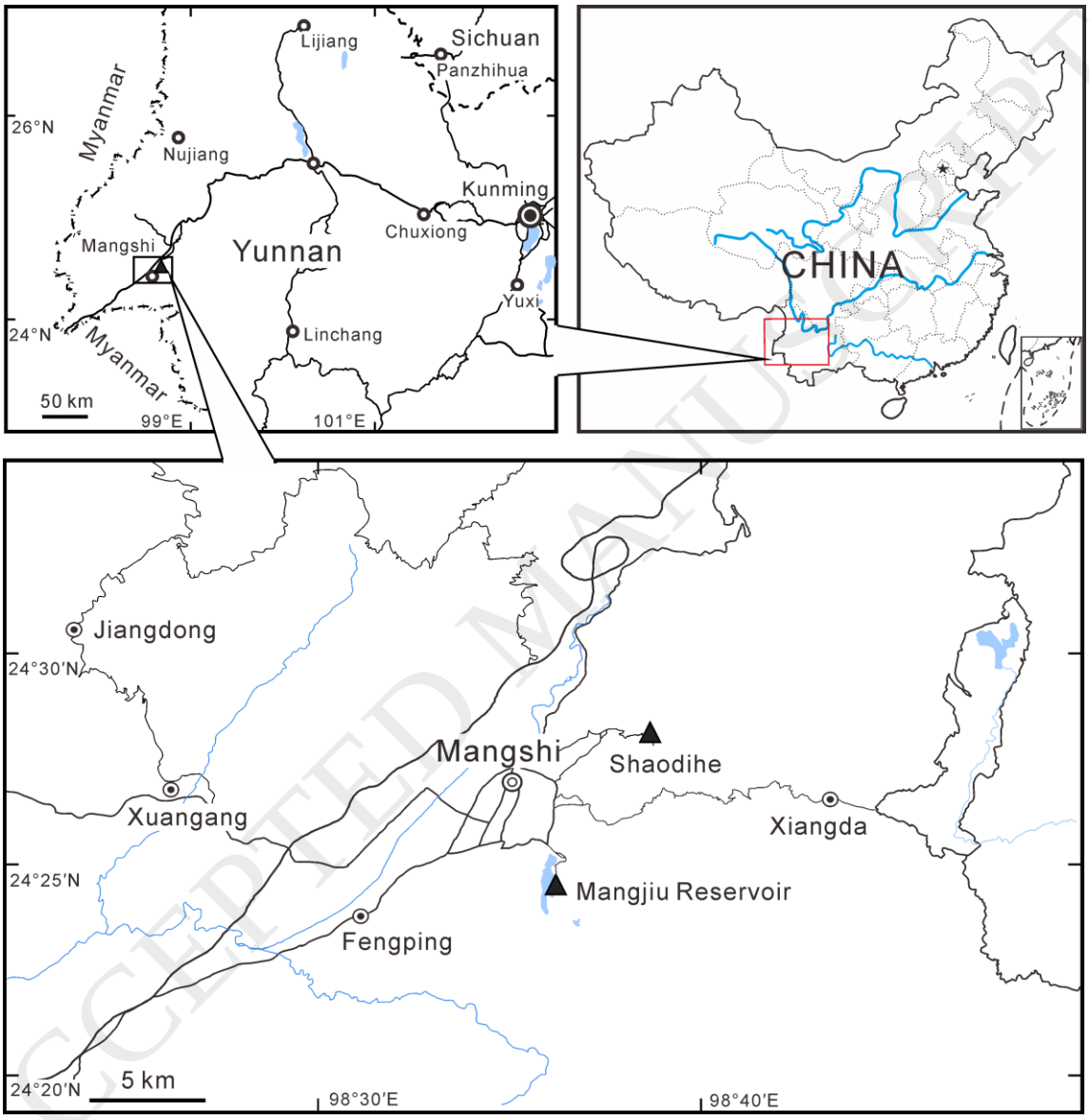

Fig. 2. The occurrence of the *Hirnantia* fauna in the upper part of the Wanyaoshu Formation in the Shaodihe section, Mangshi City, western Yunnan, Southwest China.

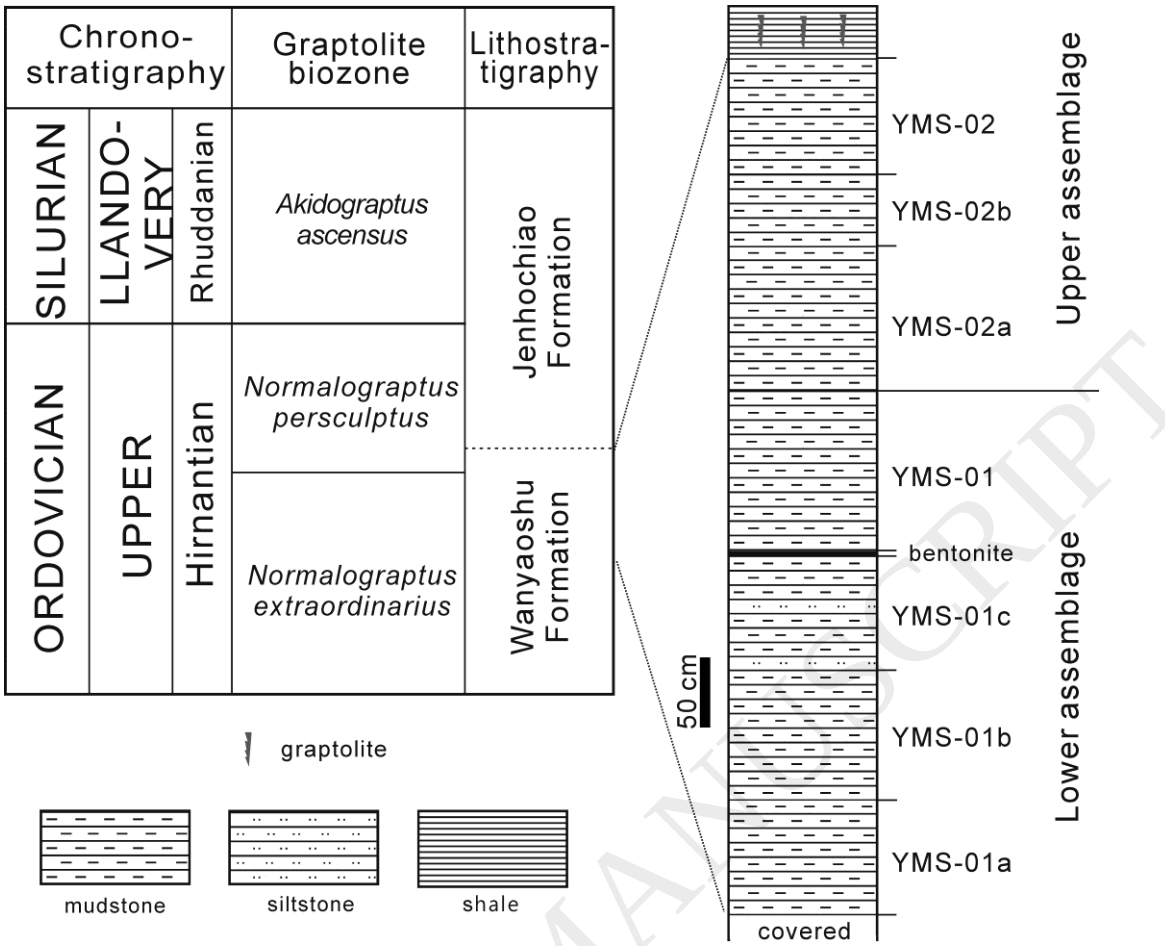

Fig. 3. Paleogeographic map displaying the positions of the five localities yielding the *Hirnantia* fauna. Map revised from Torsvik and Cocks, 2017. The position of Kazakhstan follows Cocks and Rong, 2008. Network Analysis for *Hirnantia* fauna from western Yunnan (Sibumasu terrane), Mandalay (Sibumasu terrane), Yichang (South China paleoplate), Xainza (Lhasa paleoplate), and Chu-Ili (Kazakhstan) demonstrates the close relationship between these paleoplates and terranes.

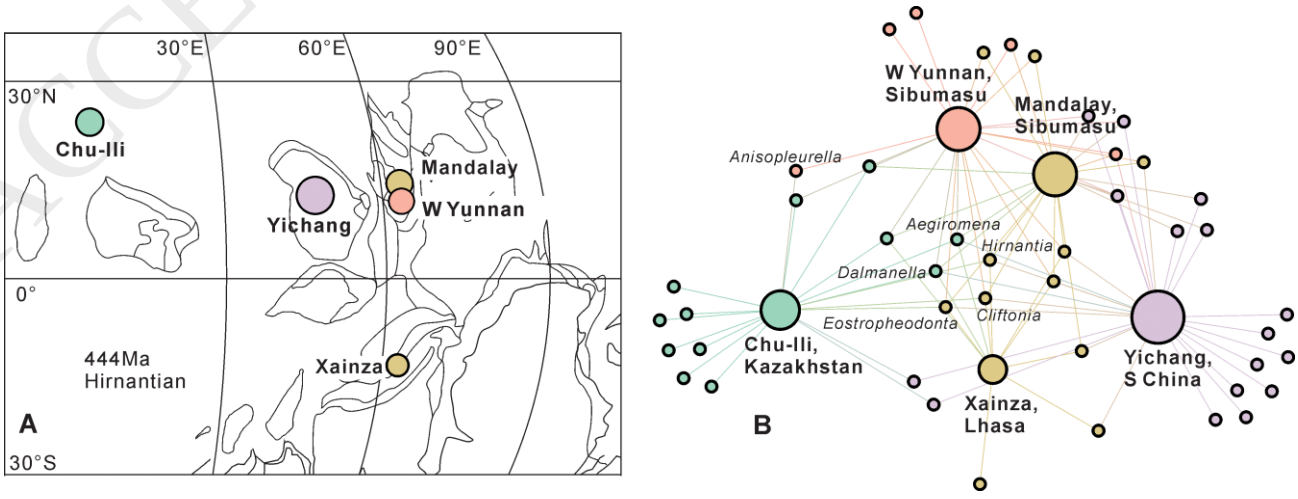

Fig. 4. Network Analysis (A) and NMDS (B) (with the Raup-Crick index) for *Hirnantia* faunas from western Yunnan (Sibumasu terrane), Mandalay (Sibumasu terrane), Yichang (South China paleoplate), Xainza (Lhasa paleoplate), Chu-Ili (Kazakhstan), and Bohemia (Prague Basin) demonstrate the close relationship between these paleoplates and terranes.

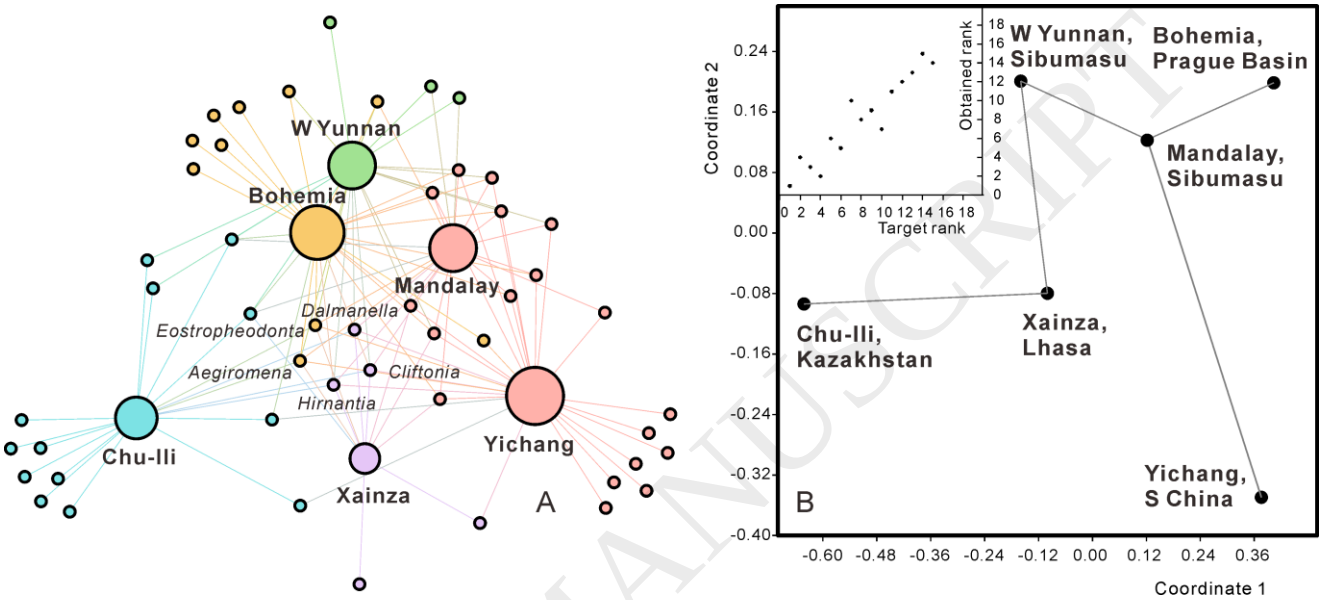

Fig. 5. (A) *Pseudopholidops partibilis* (Rong, 1979), from YMS-02, NIGP 169084, dorsal internal mould. (B–D, G) *Xenocrania haimei* (Reed, 1915), all from YMS-02, (B) NIGP 169085, dorsal internal mould; (C, D, G) NIGP 169086, dorsal external mould (G), its latex cast (D) and enlargement showing details of ornamentation (C). (E, F) *Petrocrania* sp., both from YMS-02; (E) NIGP 169087, dorsal external mould; (F) NIGP 169088, dorsal internal mould. Scale bars represent 2 mm unless otherwise noted.

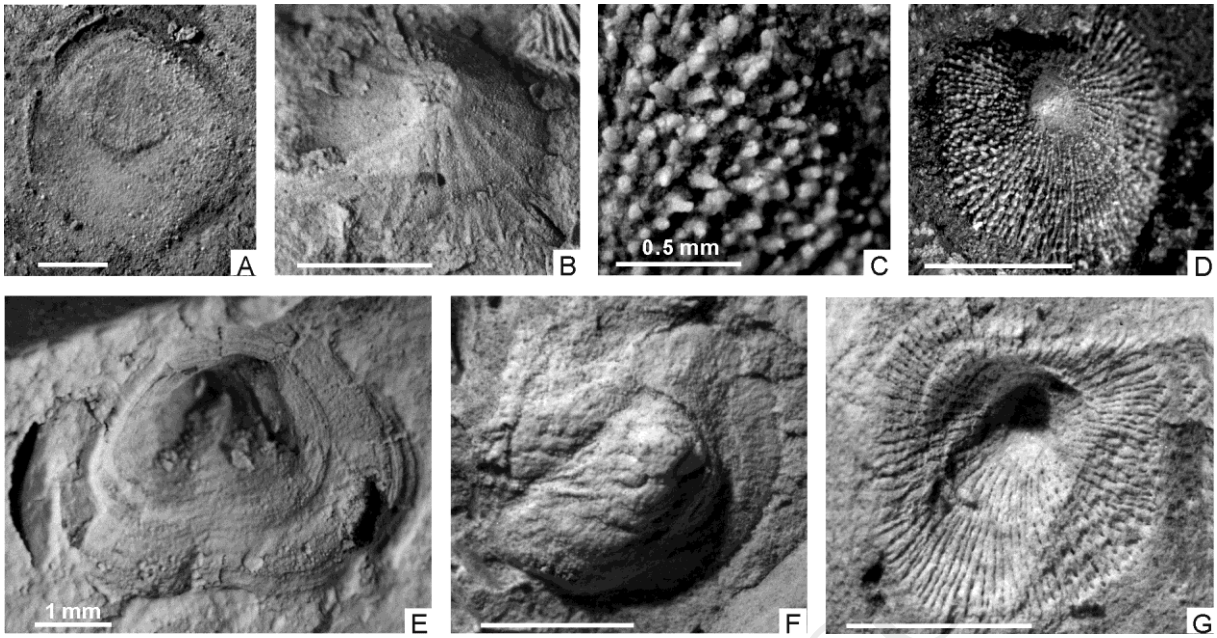

Fig. 6. (A–F) *Leptaena rugosa* Dalman, 1828; (A, B, E) NIGP 169089, 169090, 169093, three ventral internal moulds, (A) from YMS-02b, (B, E) from YMS-02; (C) NIGP 169091, dorsal external mould; (D, F) NIGP 169092, 169094, two dorsal internal moulds, (D) from YMS-02 and (F) from ACJ-906. (G–O) *Paromalomena mcmahoni* (Reed, 1915); (G, H) NIGP 169095, from YMS-01, ventral internal mould (G) and its latex cast (H); (I) NIGP 169096, from YMS-01, ventral internal mould; (J–L) NIGP 169097–169099, three dorsal internal moulds, (J, L) from YMS-02, (K) from YMS-01; (M–O) NIGP 169100, from YMS-01, dorsal internal mould (M), its latex cast (O) and that enlargement (N) showing details of cardinal process. Scale bars represent 2 mm unless otherwise noted.

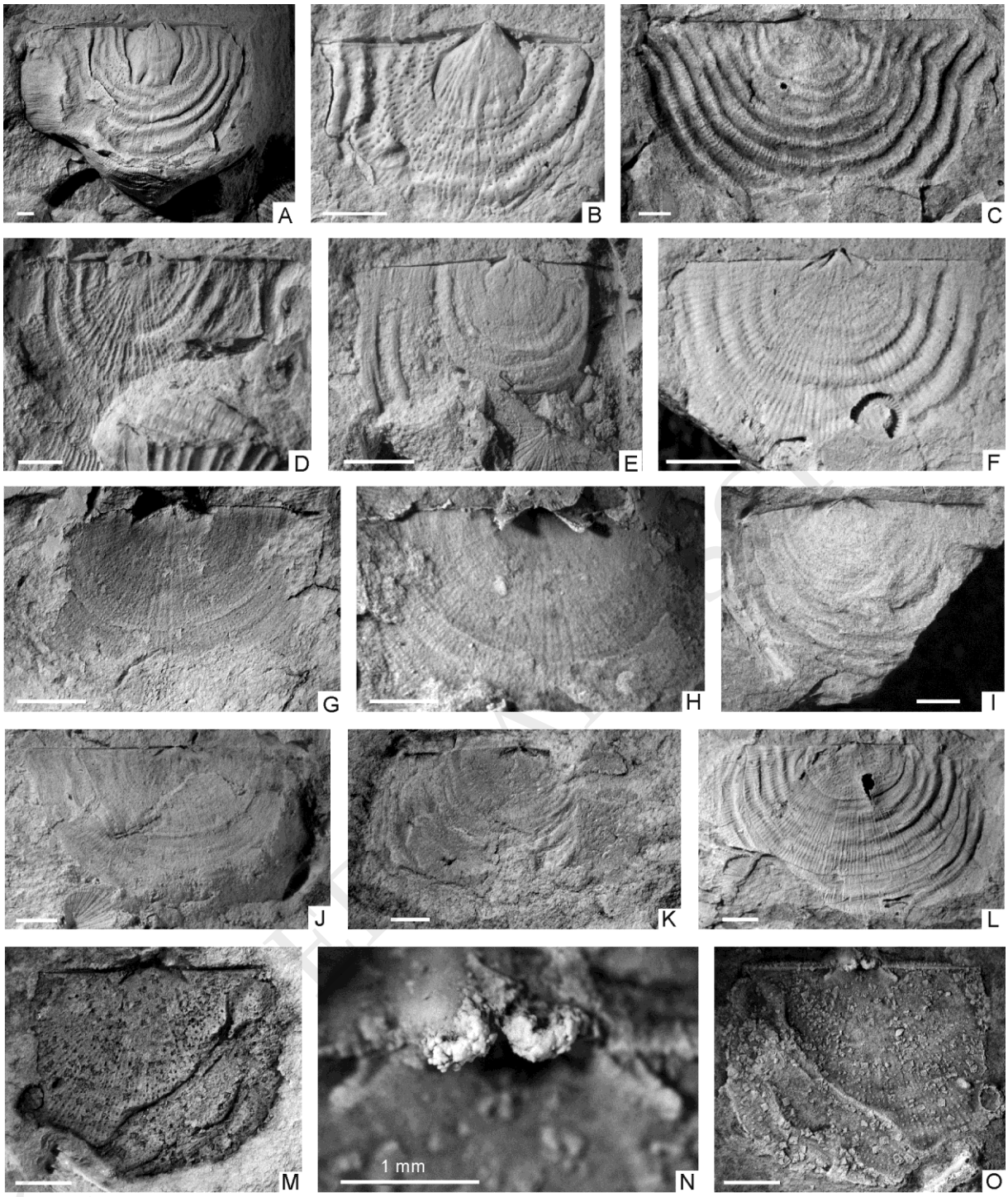

Fig. 7. (A–C) *Eostropheodonta hirnantensis* M'Coy, 1851; (A) NIGP 169101, form ACJ-906, ventral internal mould; (B, C) NIGP 169102, 169103, two dorsal internal moulds, (B) from YMS-02a and (C) from ACJ-906. (D–F) *Palaeoleptostrophia* sp.; (D, E) NIGP 169104, from YMS-02, ventral internal mould (D) and its enlargement (E) showing absence of dental plates; (F) NIGP 169105, from YMS-02, ventral internal mould. Scale bars represent 2 mm.

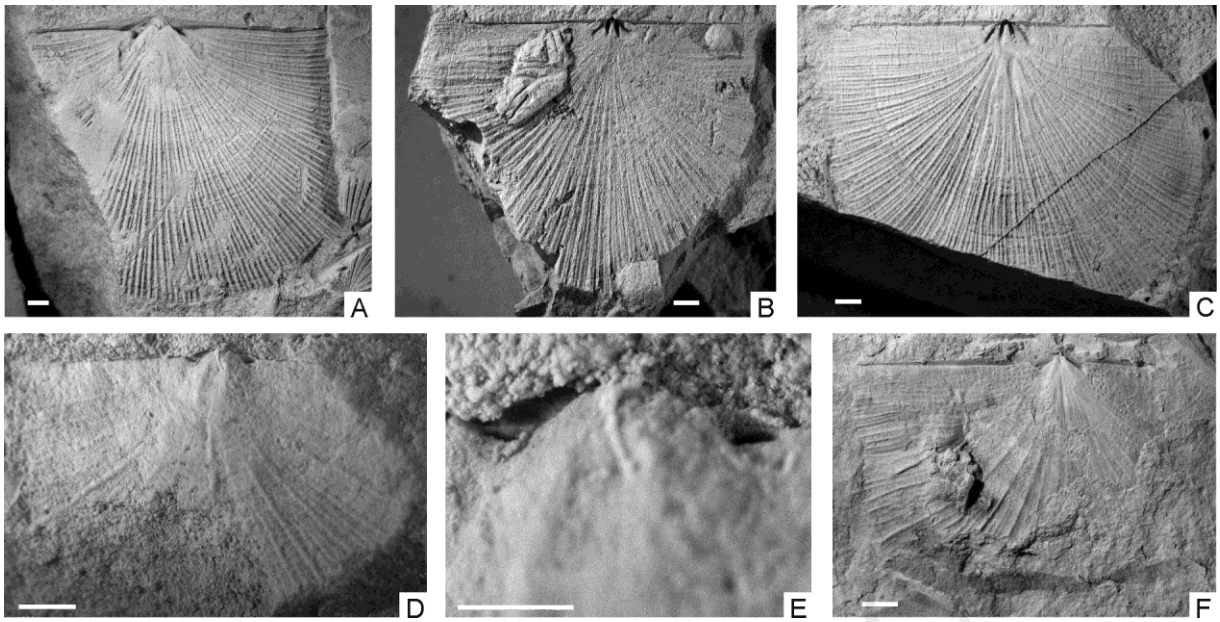

Fig. 8. (A–H) *Anisopleurella asiatica* Rong et al., 2013, all from YMS-02; (A, B) NIGP 169106, ventral internal mould (A) and its latex cast (B); (C) NIGP 169107, ventral internal mould; (D, E) NIGP 169108, dorsal internal mould (D) and its latex cast (E); (F) NIGP 169109, dorsal internal mould; (G, H) NIGP 169110, 169111, two dorsal external moulds. (I–O) *Aegiromena* (*Aegiromenella*) cf. *planissima* Reed, 1915, all from YMS-02; (I) NIGP 169112, ventral internal mould; (J, K) NIGP 169113, ventral internal mould (J) and its latex cast (K); (L) NIGP 169114, dorsal internal mould; (M, N) NIGP 169115, dorsal internal mould (M) and its latex cast (N); (O) NIGP 169116, ventral external mould. Scale bars represent 2 mm unless otherwise noted.

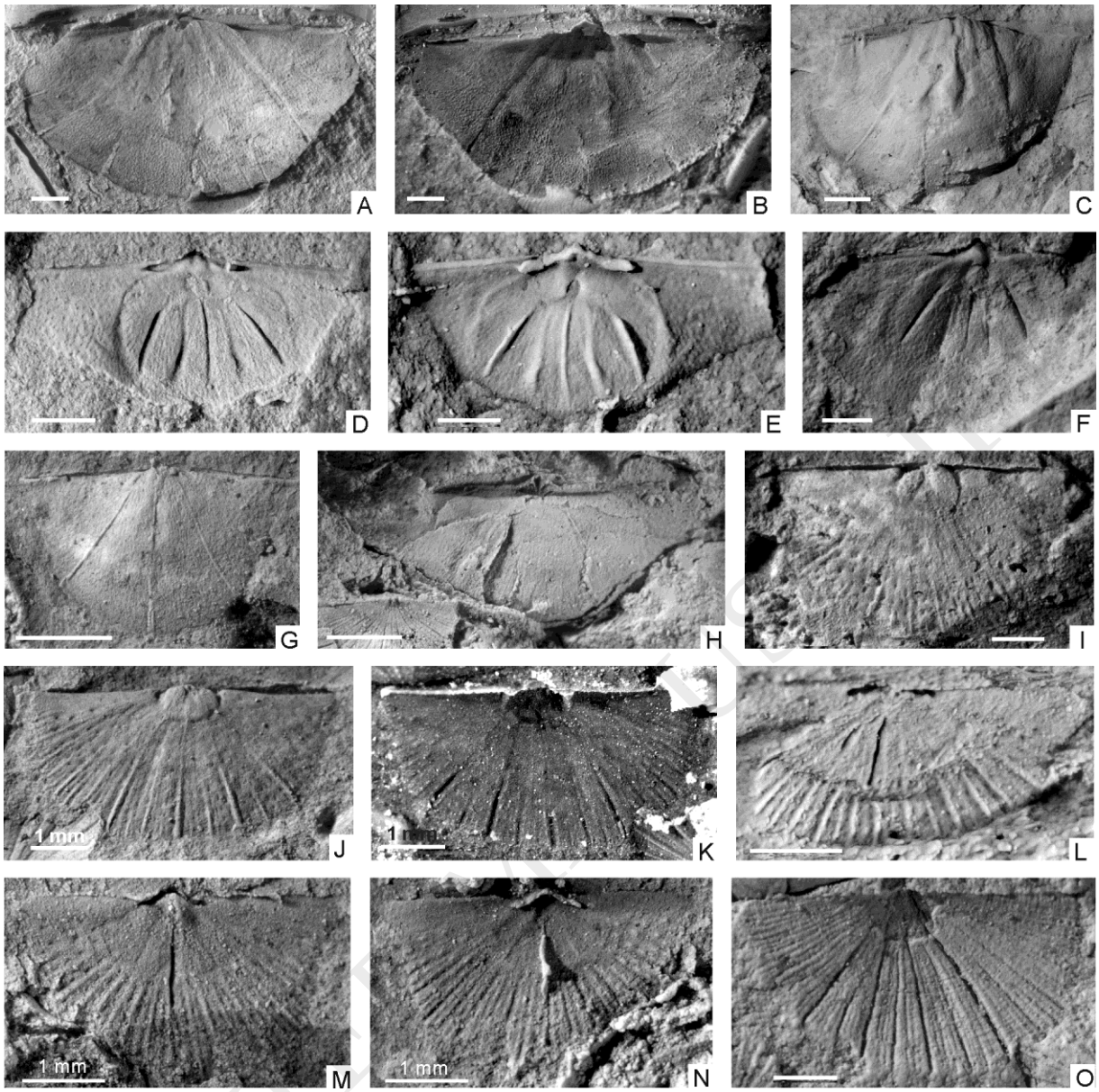

Fig. 9. Scatter diagram showing regression analysis for shell measurements of *Aegiromena* (*Aegiromenella*) cf. *planissima*.

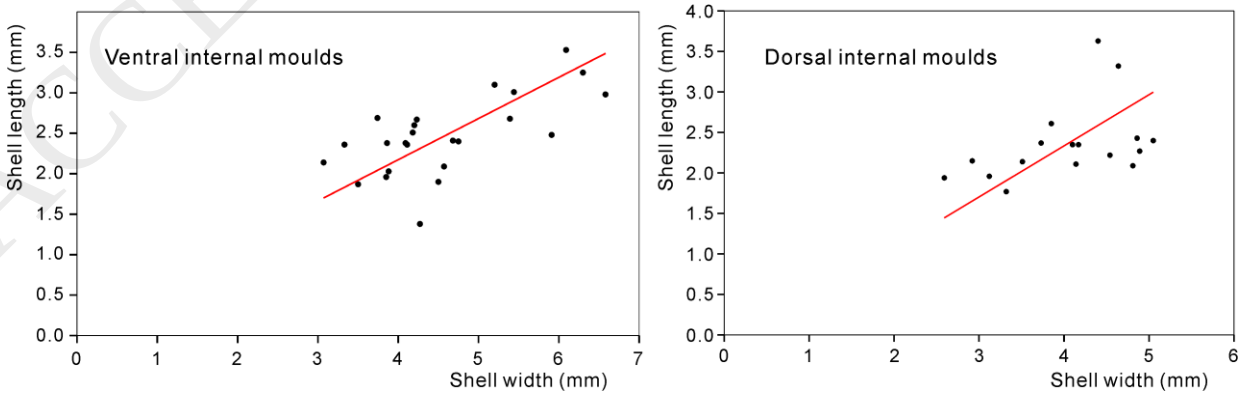

Fig. 10. Scatter diagram showing regression analysis for shell measurements of *Anisopleurella asiatica*.

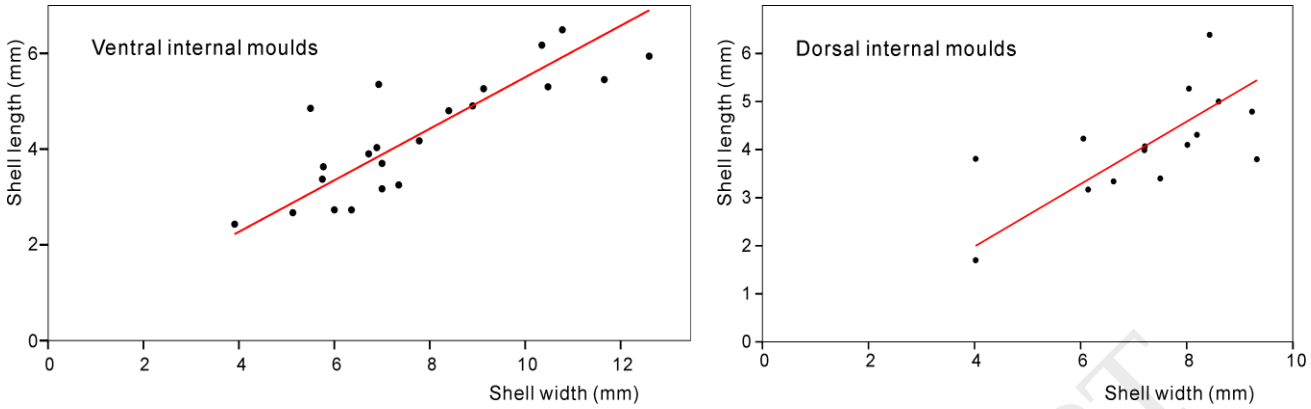

Fig. 11. (A–K) *Fardenia* (*Coolinia*) cf. *dalmani* Bergström, 1968; (A) NIGP 169117, from ACJ-906, ventral internal mould; (B) NIGP 169118, from ACJ-906, dorsal internal mould; (C) NIGP 169119, from YMS-02a, dorsal external mould; (D) NIGP 169120, from YMS-01, ventral internal mould; (E–H) NIGP 169121, 169122, both from YMS-01, dorsal (upper) and ventral (lower) internal moulds (F), latex cast of ventral internal mould (E), latex cast of dorsal internal mould (G) and its enlargement (H) showing details of cardinalia; (I–K) NIGP 169123, from YMS-01, external mould (J) and latex cast (K), the enlargement of latex cast (I) showing details of ornamentation. (L–O) *Cliftonia* cf. *psittacina* (Wahlenburg, 1821), NIGP 169124, form YMS-01b, dorsal internal mould (L), its latex cast (M) with local enlargement (N) showing detail of cardinal process, and its external mould (O). Scale bars represent 2 mm.

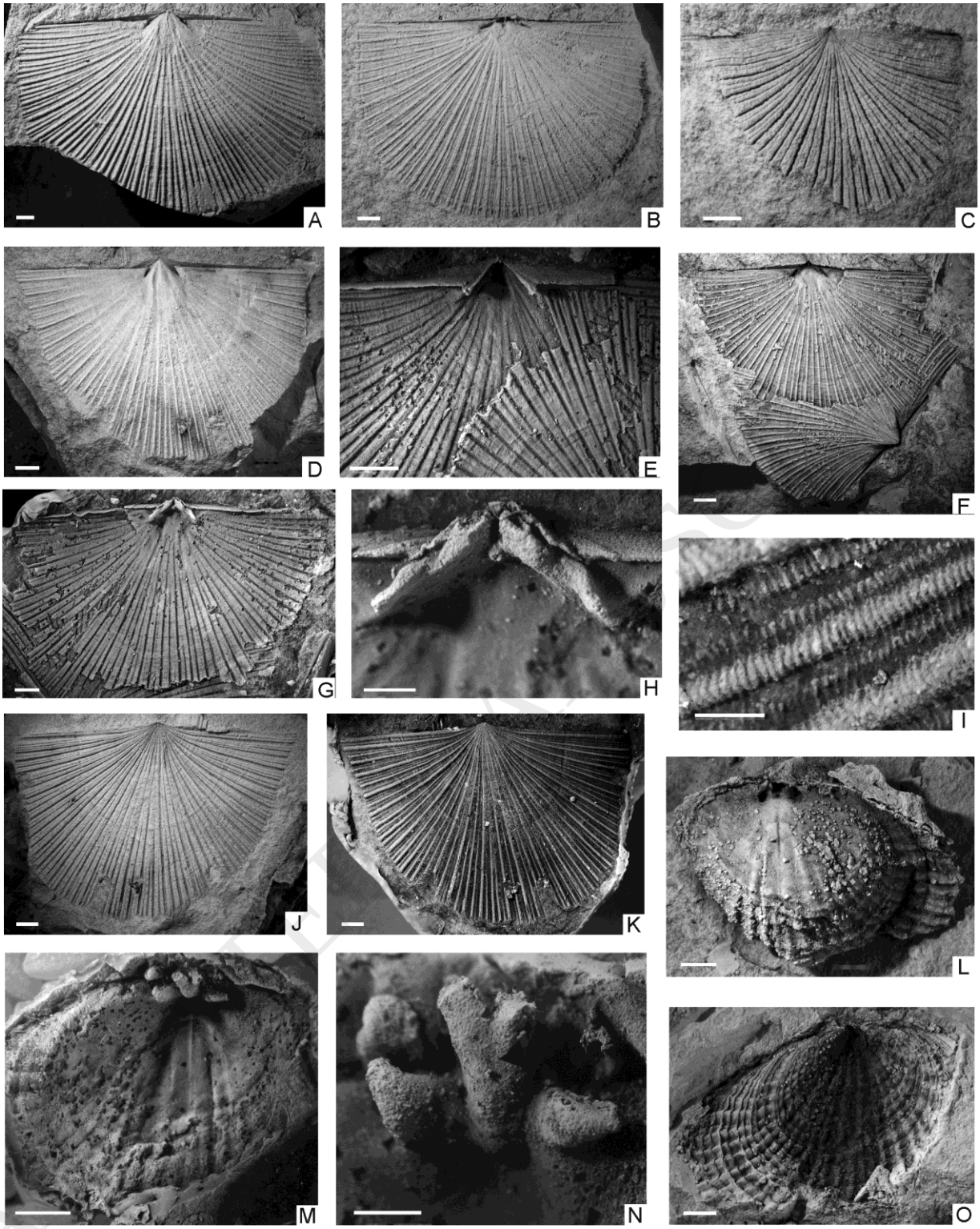

Fig. 12. Scatter diagram showing regression analysis for shell measurements of *Fardenia* (*Coolinia*) cf. *dalmani*.

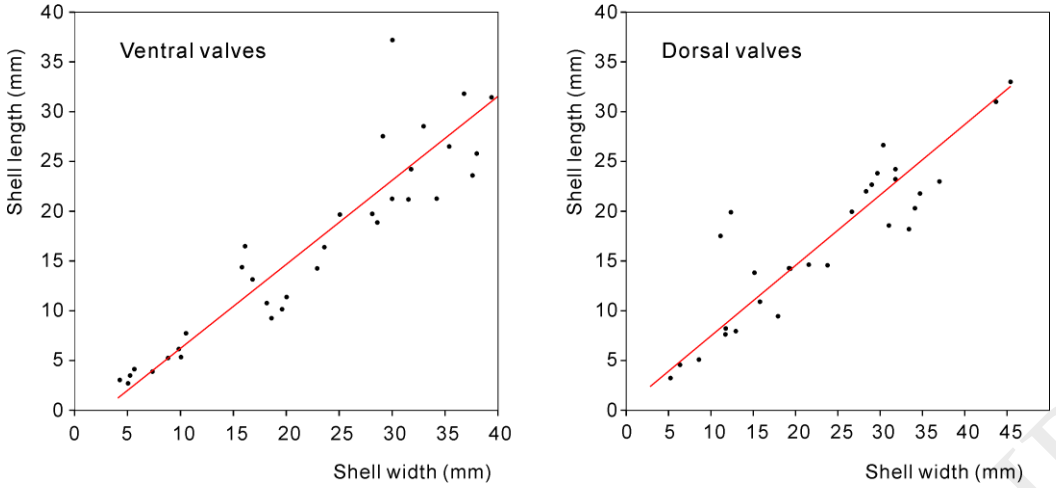

Fig. 13. (A) *Skenidioides* cf. *scoliodus* Temple, 1968, NIGP 169125, from YMS-02, dorsal internal mould. (B) *Toxorthis*? sp., NIGP 169126, from YMS-02, ventral internal mould. (C, F) *Giraldibella* sp., NIGP 169127, 169130, ventral (C) (from YMS-02) and dorsal (F) (from YMS-02) internal moulds. (D, E) *Dolerorthis*? sp., NIGP 169128, 169129, both from YMS-02, ventral (D) and dorsal (E) internal moulds. (G–J) *Templeella* cf. *gobiensis* Rozman and Rong 1993; (G) NIGP 169131, from YMS-02, ventral internal mould; (H, I) NIGP 169132, from YMS-02, dorsal internal mould (H) and its enlargement (I) showing cardinalia and muscle field; (J) NIGP 169133, from YMS-02, dorsal internal mould. (K–R) *Dalmanella testudinaria* (Dalman, 1828), all from YMS-02, except (L) from ACJ-906; (K) NIGP 169134, ventral internal mould; (L–N) NIGP 169135–167137, dorsal internal moulds; (O) NIGP 169138, ventral internal mould; (P, Q) NIGP 169139, dorsal internal mould (P) and its latex cast (Q); (R) NIGP 169140, dorsal external mould. Scale bars represent 2 mm unless otherwise noted.

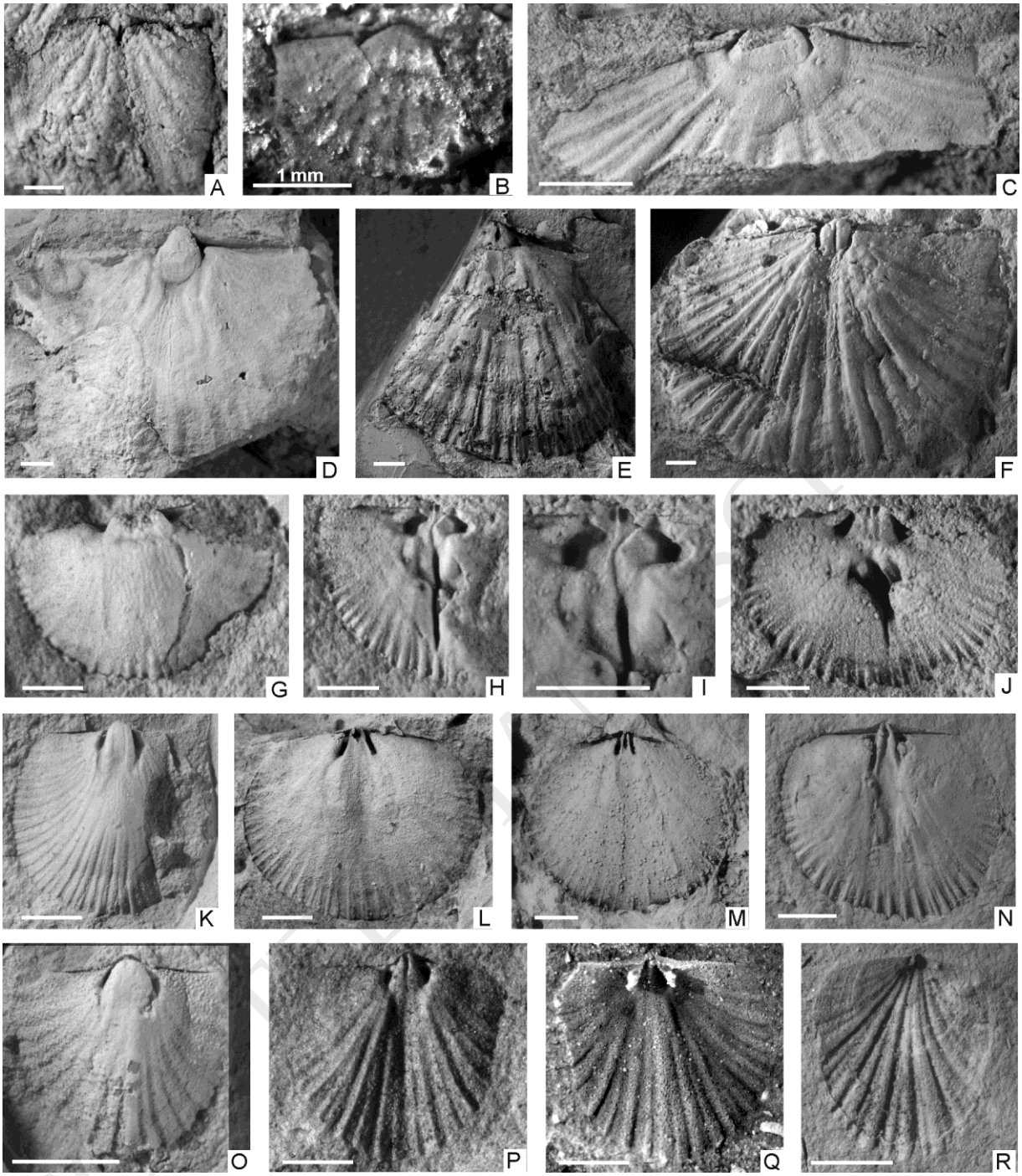

Fig. 14. Scatter diagram showing regression analysis for shell measurements of *Hirnantia sagittifera*.

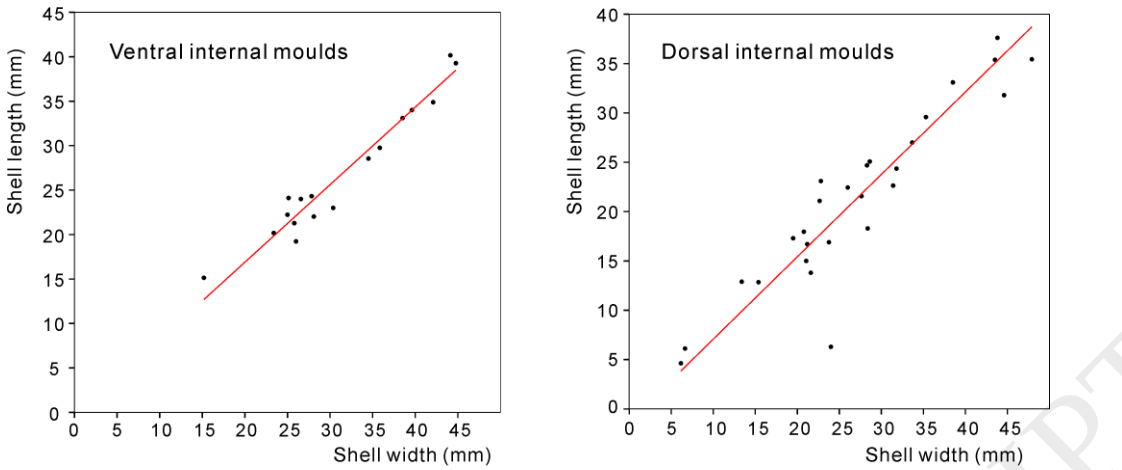

Fig. 15. (A–D) *Kinnella medlicotti* (Reed, 1915); (A) NIGP 169141, from YMS-01, ventral internal mould; (B) NIGP 169142, from YMS-01b, dorsal internal mould; (C, D) NIGP 169143, from YMS-01a, dorsal internal mould (C) and its latex cast (D). (E, F) *Draborthis caelebs* Marek and Havlíček, 1967; (E) NIGP 169144, from YMS-02, ventral internal mould; (F) NIGP 169145, from ACJ-906, dorsal internal mould. (G–R) *Hirnantia sagittifera* (M'Coy, 1851); (G, H) NIGP 169146, from YMS-01, ventral internal mould (G) and its latex cast (H); (I, J) NIGP 169147, from YMS-01b, ventral internal mould (I) and its latex cast (J); (K) NIGP 169148, from YMS-01b, ventral internal mould; (L) NIGP 169149, from YMS-01b, dorsal internal mould; (M, P) NIGP 169151, from YMS-01, dorsal internal mould (P) and its latex cast of cardinalia (M); (N, O) NIGP 169150, from YMS-01a, dorsal internal mould (N) and its latex cast (O); (Q) NIGP 169152, from YMS-01a, dorsal internal mould; (R) NIGP 169153, from YMS-01, latex cast of dorsal external mould. Scale bars represent 2 mm.

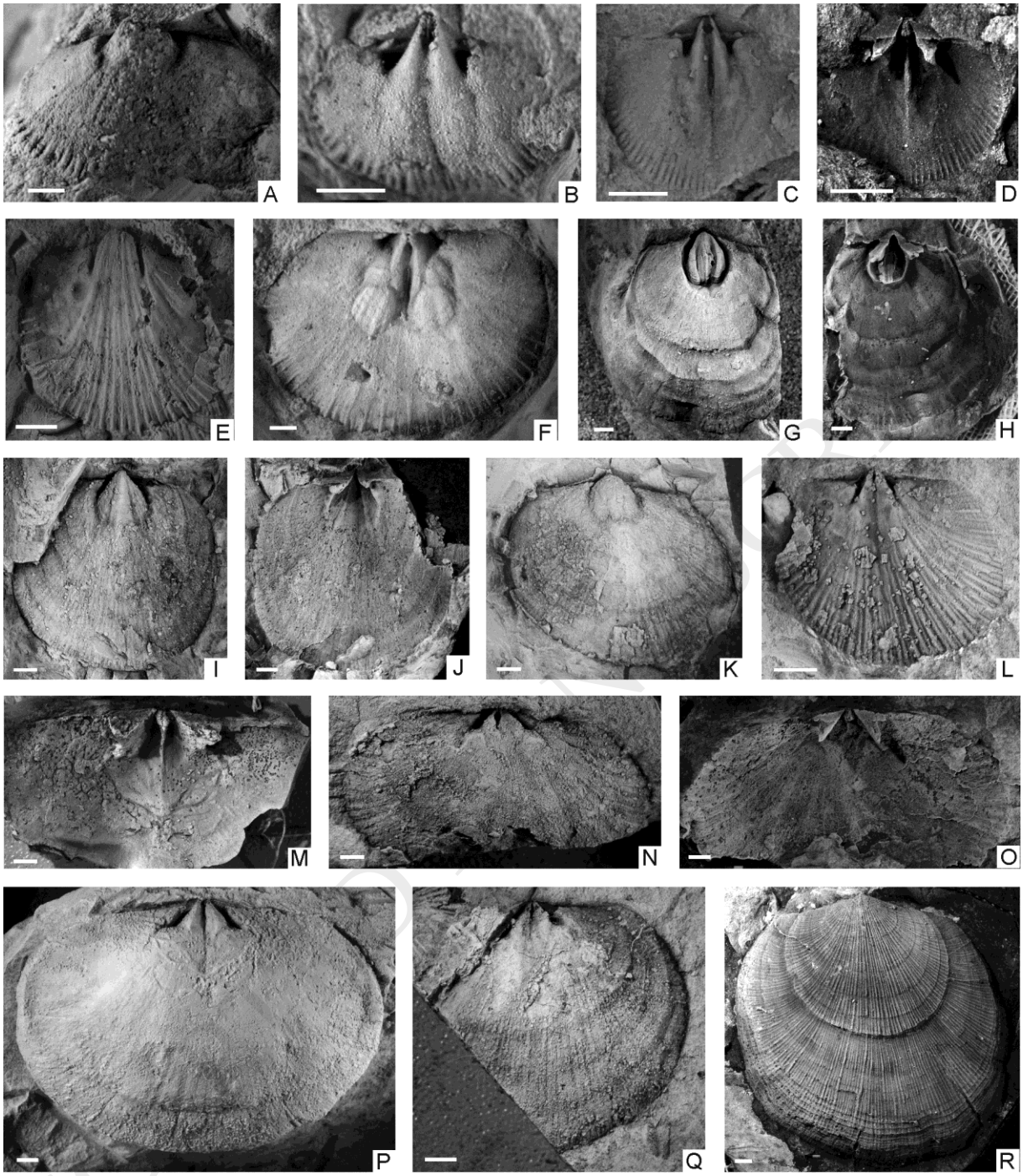

Fig. 16. (A–H) *Plectothyrella crassicostis* (Dalman, 1828), all from YMS-01; (A, B) NIGP 169154, ventral internal mould (A) and its latex cast (B); (C–F) NIGP 169155, dorsal internal mould (C) and its latex cast (D), lateral view (E) and anterior view (F) of the enlargement of latex cast showing the details of cardinalia; (G, H) NIGP 169156, ventral internal mould (G) and its latex cast (H). (I–M) *Hindella crassa* (Sowerby, 1839), all from YMS-01, except (J) from YMS-02; (I) NIGP 169157, ventral internal mould; (J, M) NIGP 169158, 169160, two dorsal internal moulds; (K, L) NIGP 169159,

ventral internal mould (K) and its latex cast (L). Scale bars represent 2 mm.

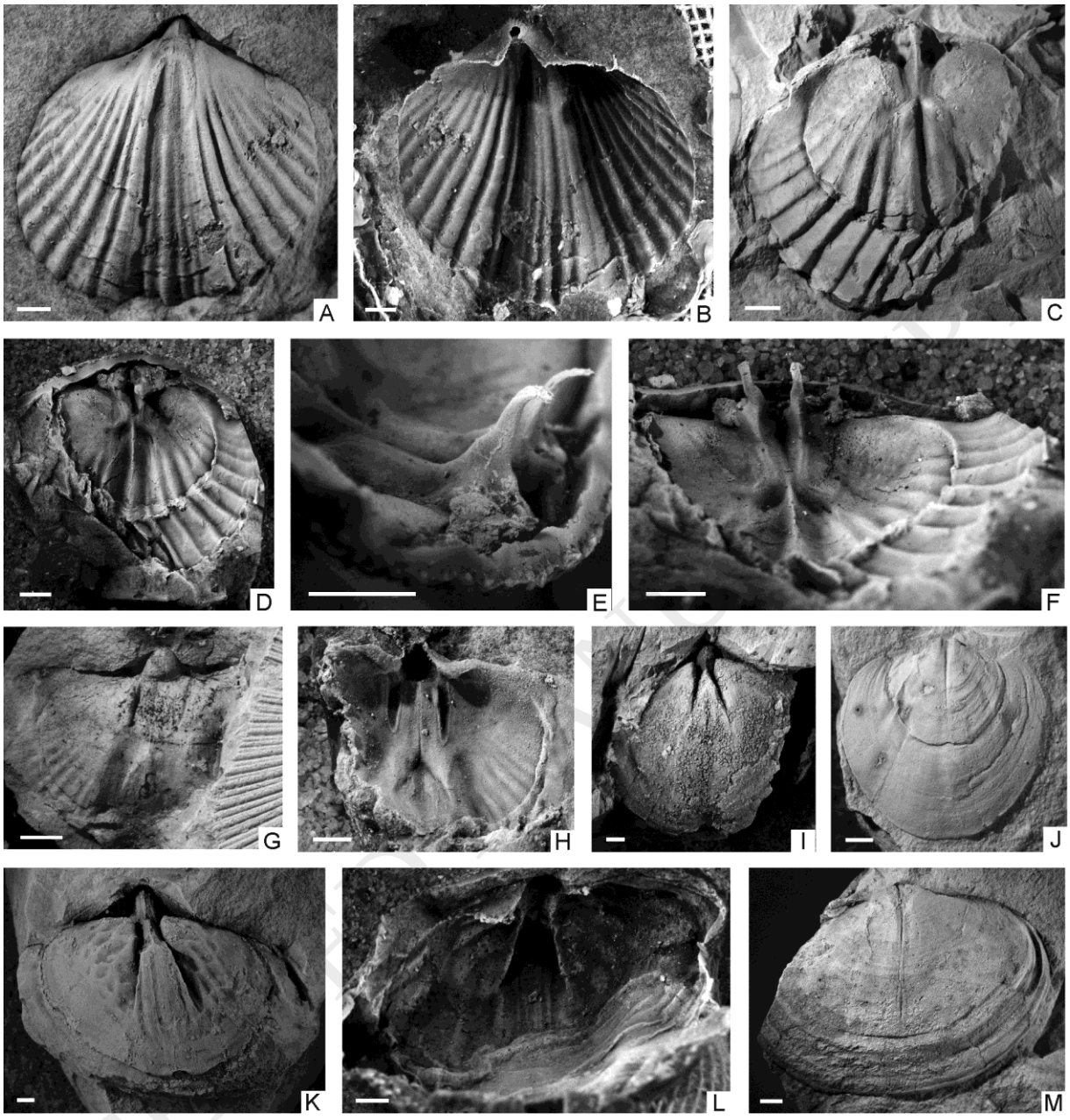

Table 1. Measurements (in mm) of *Aegiromena* (*Aegiromenella*) cf. *planissima*. Abbreviations: L. Mus. and W. Mus., L. Car. and L. Med. represent length and width of the ventral muscle field and length of dorsal cardinalia and median ridges respectively; S. dev. represents standard deviation.

Sum	Ventral internal moulds				Dorsal internal moulds			
N = 42	Width	Length	W. Mus.	L. Mus.	Width	Length	L. Car.	L. Med.
Min	3.07	1.38	0.50	0.30	2.59	1.77	0.69	0.65
Max	6.58	3.53	1.49	1.02	5.05	3.63	1.40	2.12
Mean	3.07	1.38	0.50	0.30	4.04	2.36	1.00	1.41
S. dev.	0.96	0.49	0.25	0.17	0.75	0.47	0.20	0.35

Table 2. Measurements (in mm) of *Anisopleurella asiatica*. Abbreviations: L. Bema and W. Bema represent length and width of bema respectively; S. dev. represents standard deviation.

Sum N = 37	Ventral internal moulds		Dorsal internal moulds			
	Width	Length	Width	Length	W. Bema	L. Bema
Min	4.05	2.64	4.02	1.70	1.72	0.44
Max	12.6	6.49	9.32	6.39	6.11	2.43
Mean	7.75	4.29	7.24	4.09	4.46	1.40
S. dev.	2.28	1.23	1.64	1.06	1.15	0.49

Table 3. Measurements (in mm) of *Fardenia* (*Coolinia*) cf. *dalmani*. Abbreviations: L. Den. and W. Den., L. Car. and L. Car. represent length and width of the ventral dental plates and dorsal cardinalia respectively; S. dev. represents standard deviation.

Sum	Ventral internal moulds				Dorsal internal moulds			
N = 41	Width	Length	W. Den.	L. Den.	Width	Length	W. Car.	L. Car.
Min	4.05	2.64	0.77	0.34	5.22	3.24	1.72	0.44
Max	39.4	37.2	8.65	6.77	45.40	32.20	6.11	2.43
Mean	21.72	16.67	4.04	2.01	26.45	19.56	4.46	1.40
S. dev.	11.94	10.30	2.25	1.63	11.83	7.87	1.15	0.49

Table 4. Measurements (in mm) of *Hirnantia sagittifera*. Abbreviations: L. Mus. and W. Mus., L. Car. and L. Car. represent length and width of the ventral muscle field and dorsal cardinalia, respectively; S. dev. represents standard deviation.

Sum	Ventral internal moulds				Dorsal internal moulds			
N = 45	Width	Length	W. Mus.	L. Mus.	Width	Length	W. Car.	L. Car.
Min	15.19	15.14	3.16	3.64	6.64	4.63	1.04	0.81
Max	44.76	40.16	12.13	12.63	47.90	37.61	11.53	6.43
Mean	31.34	26.78	6.74	8.28	27.13	21.54	5.51	3.37
S. dev.	8.36	7.29	1.99	2.63	10.71	8.72	2.08	1.38